

Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 2. *Palaemonetes (Palaemonetes) varians* (Leach, 1814) and morphological variation

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Synopsis

Five larval and selected post larval stages of *Palaemonetes (Palaemonetes) varians* are described from specimens reared in the laboratory. The rate of larval development and the effect of desynchronization of epigenesis and moulting are discussed. Analysis of morphometric and meristic variation showed that normalizing selection may result in a reduction in variation of larval size distribution at metamorphosis. No such reduction in variation of meristic characters was found. A significant increase in variation of the exopodite of the mouthpart maxilla 2 was recorded from the closely related palaemonid *Palaemon (Palaeander) elegans*. The significance of these results is discussed with reference to the life histories of these shrimps.

Introduction

Palaemonetes (Palaemonetes) varians or the ditch shrimp has been the subject of larval development studies for nearly 140 years (see synopsis of larval data, below). The species is reared easily in the laboratory and this explains, to some extent, its popularity. It was cited as an example of poecilogony (Boas, 1889) or larval polymorphism, until Sollaud (1923a) showed that there were, in fact, different species in northern and southern Europe and in North Africa but that co-existence occurred. Heldt (1953) revived the controversy after examining samples of *P. (P.) varians* from Lake Kelbia in Tunis. In different salinities Heldt reported that '... ces larves différentes, issues de ces deux sortes d'œufs, aboutissent . . . à des adultes morphologiquement identiques'. It is, however, not difficult to see why the concept of poecilogony has been applied to this species which does, apparently, show considerable phenotypic variation during larval development and metamorphosis.

A species is often characterized solely by genotype and phenotype in discussions on development. Waddington (1953) developed a further concept – the *epigenotype* which he defined as '... the system of causal relations by which the newly fertilized zygote . . . becomes realized as the fully developed adult'. He distinguished between normalizing selection in which phenotypes resulting directly from the presence of an abnormal gene were removed from a population, and stabilizing selection which involved the removal of phenotypes disadvantaged by an unstable epigenetic system.

In this context morphometric and meristic data for larval stages of *Palaemonetes (Palaemonetes) varians* were pooled and analysed to see if epigenetic development in shrimps followed the same pattern reported recently in the development of newts (Bell, 1974, 1975), when a decrease in morphological variation was recorded as the animals approached metamorphosis.

Materials and methods

Rearing

Ovigerous *Palaemonetes (Palaemonetes) varians* (Leach) were collected in July 1976 by handnetting from ditches alongside the estuary at Burnham-on-Crouch, Essex, England (grid reference

TQ 943957). Rearing techniques, similar to those reported previously (Fincham, 1977), were used with the following modifications:

1. The constant temperature room was at 22 ± 0.5 °C; 2 °C below the temperature of the water in the ditches where the collections were made.
2. No mass cultures were set up in order to eliminate the problems of identifying later zoeal stages where moulting history was not available. To ensure, however, that adequate material was available for drawing and assessing morphological variation, eight compartmented trays were set up, containing 144 larvae. At each zoeal stage, 10 larvae, their moults, and a further 10 moults from other individuals, were preserved.
3. All trays and equipment were sterilized with boiling water before use to prevent the accumulation of bacteria.

Larval material has been deposited in the Crustacea collection of the BM(NH), registration number 1977 : 284.

Analysis of morphometric and meristic variation

Ten moults and larvae were examined at each stage to determine the range of overall size and also of setal numbers on selected appendages. Mean (\bar{x}) and standard deviation (*s.d.*) were calculated for each character at the different stages. To test if there was a genuine increase in variation other than an increase expected from animals of greater size, coefficients of variation ($100 \times s.d./\text{mean}$) were calculated.

Palaemonetes (Palaemonetes) varians (Leach, 1814)

Palaemon varians Leach, 1814.

Palaemon variabilis Bouchard-Chantereaux, 1829.

Palaemonetes varians microgenitor Boas, 1889.

Palaemonetes varians occidentalis Sollaud, 1923.

Palaemonetes (Palaemonetes) varians Holthuis, 1949.

SYNOPSIS OF LARVAL DATA FROM PUBLISHED WORK. *Palaemon variabilis*: Du Cane, 1839 (zoeae 1–4, dorsal, lateral views, plankton, British waters); *Palaemonetes varians*: Boas, 1880 (selected appendages of some zoeae, Danish waters); Mayer, 1880 (zoeae 1–4, post larvae, some dorsal, lateral views, appendages, Mediterranean waters); Weldon, 1890 (zoeae 1–3/4, no figures, laboratory reared, British waters); Allen, 1893*a, b* (development of green gland, shell gland and body cavity in larvae, laboratory reared, British waters); *P. v. microgenitor*: Sollaud, 1914 (egg size, abbreviated development and order of appendage appearance); Sollaud, 1919 (effect of environment on duration of larval life, French waters); Sollaud, 1921 (phototropism before and after metamorphosis); *P. varians*: Gurney, 1923 (breeding period, British waters); *P. v. occidentalis*: Sollaud, 1923*a* (zoeae 1–5, post larva, French waters); 1923*b* (larval polymorphism); *P. varians*: Gurney, 1924 (zoeae 1–5, post larvae, plankton and laboratory reared, British waters); Sollaud, 1930 (larval polymorphism); Heldt, 1953 (larval polymorphism); Weygoldt, 1961 (embryology, German waters); Le Roux, 1970 (effect of environment on number of larval stages, French waters).

In the following short descriptions of the key characters of the larval stages, all setal counts have been omitted but these are recorded in Table 1.

DESCRIPTION OF LARVAL STAGES

Key characters are printed in *italic type*.

ZOEA 1 (Fig. 1) 3.8 mm (3.5–4.1 mm)

Head (Figs 1*a, b*): *eyes sessile*.

Carapace (Figs 1*a, b*): *without spines*, rostrum straight, tapering distally, ventral margin with minute retrorse teeth distally.

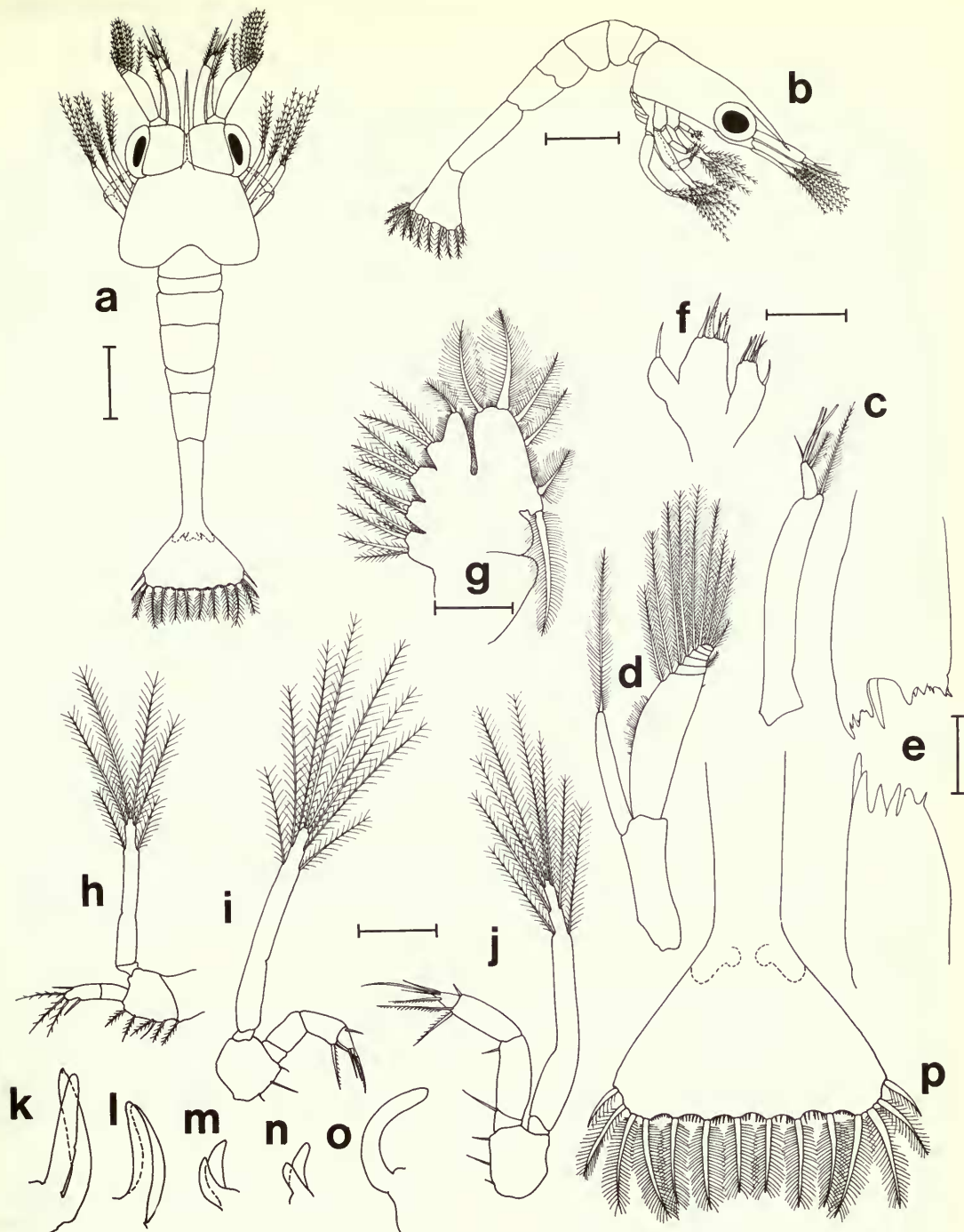


Fig. 1 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0.5 mm; c, d, h-p = 0.2 mm; g = 0.1 mm; e, f = 0.05 mm.

Antenna 1 (Fig. 1c): peduncle bearing single flagellar segment with three aesthetascs distally, one wider than the others.*

Antenna 2 (Fig. 1d): exopodite as a broad lamina divided into 5 short segments distally.

Mandibles (Fig. 1e): asymmetrical.

Maxillipeds 1-3 (Figs 1h-j): with natatory exopodites.

Pereiopods 1-4 (Figs 1k-n): *rudimentary, biramous*.

Pereiopod 5 (Fig. 1o): *rudimentary, uniramous*.

Abdomen (Figs 1a, b): somite 6 continuous with telson; pairs of ventral buds on somites 1-5 indicate position of pleopods.

Telson (Fig. 1p): fans out distally, posterior margin bears 7+7 plumose spines, with minute spines between four innermost pairs of spines.

ZOEA 2 (Fig. 2) 4.2 mm (4.0-4.5 mm)

Head (Figs 2a, b): *eyes 'stalked'*.

Carapace (Figs 2a, b): one *dorso-medial* and a pair of supraorbital spines all bent forward with small retrorse teeth ventrally, rostrum without teeth.

Antenna 1 (Fig. 2c): distal segment of peduncle bearing first segment of internal flagellum, external flagellum now with four distal aesthetascs, two wider than others.

Pereiopods 1, 2 (Figs 2k, l): *developed, with natatory exopodites*.

Pereiopods 3, 4 (Figs 2m, n): *rudimentary, biramous*.

Pereiopod 5 (Fig. 2o): *developed, uniramous* (without exopodite).

Abdomen (Figs 2a, b): *somite 5 with posterior margin produced into a pair of spines*.

Telson (Fig. 2p): *developing uropods visible beneath exoskeleton*; in central group of small spines, one pair longer than the others.

ZOEA 3 (Fig. 3) 4.6 mm (4.3-4.8 mm)

Carapace (Figs 3a, b): *two dorso-medial spines* and a small frontolateral spine at edge of carapace beneath the eyes, former with retrorse teeth ventrally.

Antenna 1 (Fig. 3c): external flagellum with three distal aesthetascs; conspicuous spine medially and stylocerite forming on proximal external margin of first segment of peduncle.

Antenna 2 (Fig. 3d): exopodite with distal part divided into only three short segments.

Pereiopods 1, 2 (Figs 3k, l): endopodite with internal distal margin of propodus produced slightly forward (will become fixed finger of chela).

Pereiopod 3 (Fig. 3m): *developed, with natatory exopodite*.

Abdomen (Figs 3a, b): *somite six divided from telson by suture*.

Telson (Fig. 3p): narrower, but still broader distally, outer pair of spines on posterior margin considerably reduced: *uropod endopodite with no marginal setae; exopodite with marginal, plumose setae*.

ZOEA 4 (Figs 4, 5) 5.2 mm (4.9-5.5 mm)

Carapace (Figs 4a, b): *three dorso-medial spines* with small retrorse teeth ventrally.

Antenna 2 (Fig. 5b): endopodite with 3-segmented flagellum (usually), as long as scaphocerite, distal part of exopodite divided into two, one or no short segments.

Pereiopods 1, 2 (Figs 5f, g): *endopodite with internal distal margin of propodus* produced forward to over half length of dactylus (excluding terminal setae).

Pereiopod 4 (Fig. 5i): developed with natatory exopodite.

Abdomen (Figs 4b, 5k-o): pleopods on somites 1-5 rudimentary, biramous.

Telson (Fig. 5p): a little broader distally than proximally, posterior margin weakly concave with 5+5 *large spines* and with 2 smaller spines on latero-distal margin; *endopodite and exopodite of uropod both with marginal plumose setae*.

ZOEA 5 (Figs 6, 7, 8) 5.8 mm (5.5-6.0 mm)

Carapace (Fig. 6b): *setae in angles of two anterior dorso-medial spines*.

* In a previous paper (Fincham, 1977) two aesthetascs were recorded distally on the flagellar segment of antenna 1 in zoea 1 of *Palaemon (Palaeander) elegans*. Examination of more material, including specimens from the Marmara Sea, Turkey, indicate that three aesthetascs is the usual number (one wide, two narrow).

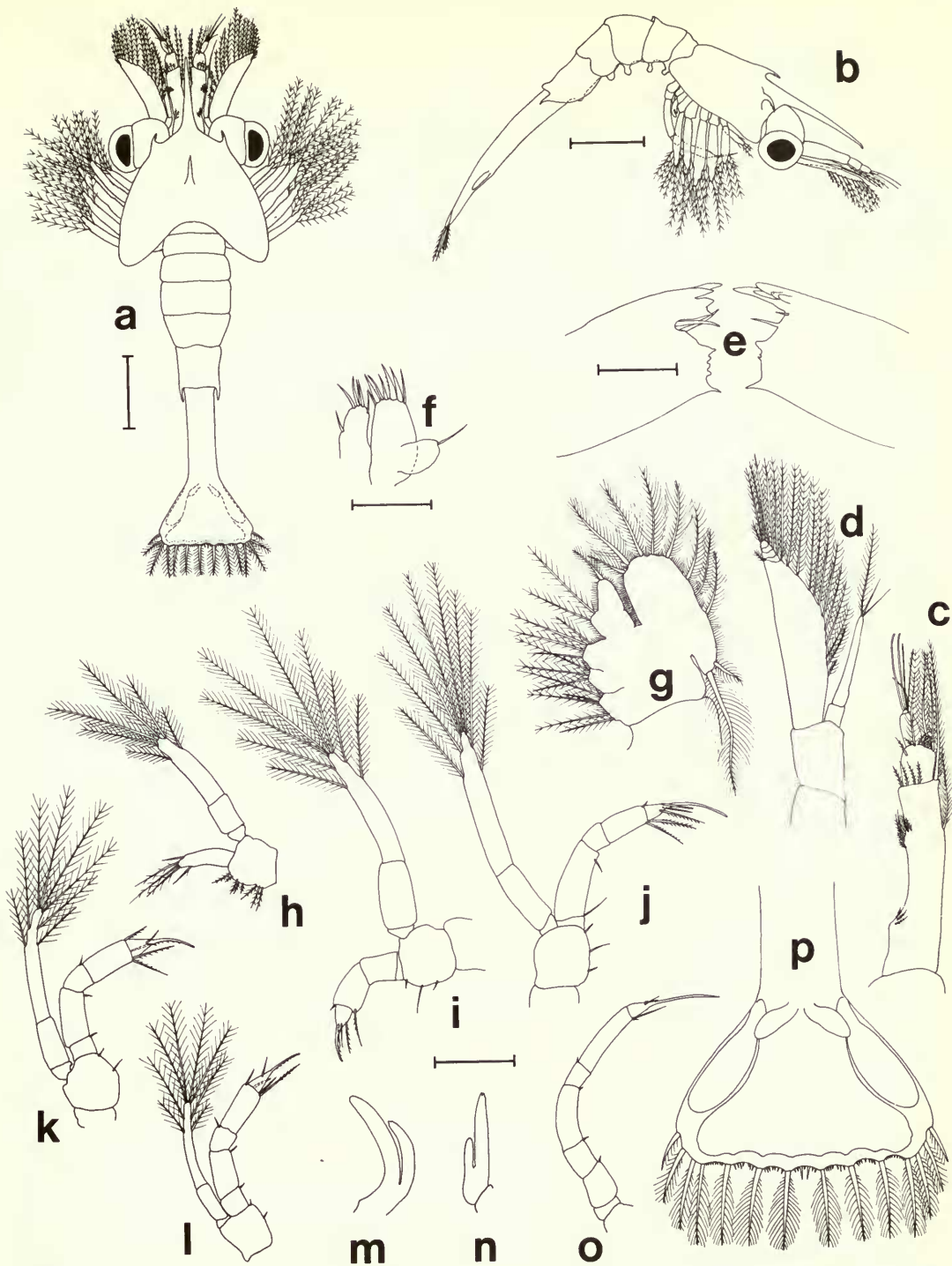


Fig. 2. Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0.5 mm; c, d, h-p = 0.2 mm; f, g = 0.1 mm; e = 0.05 mm.

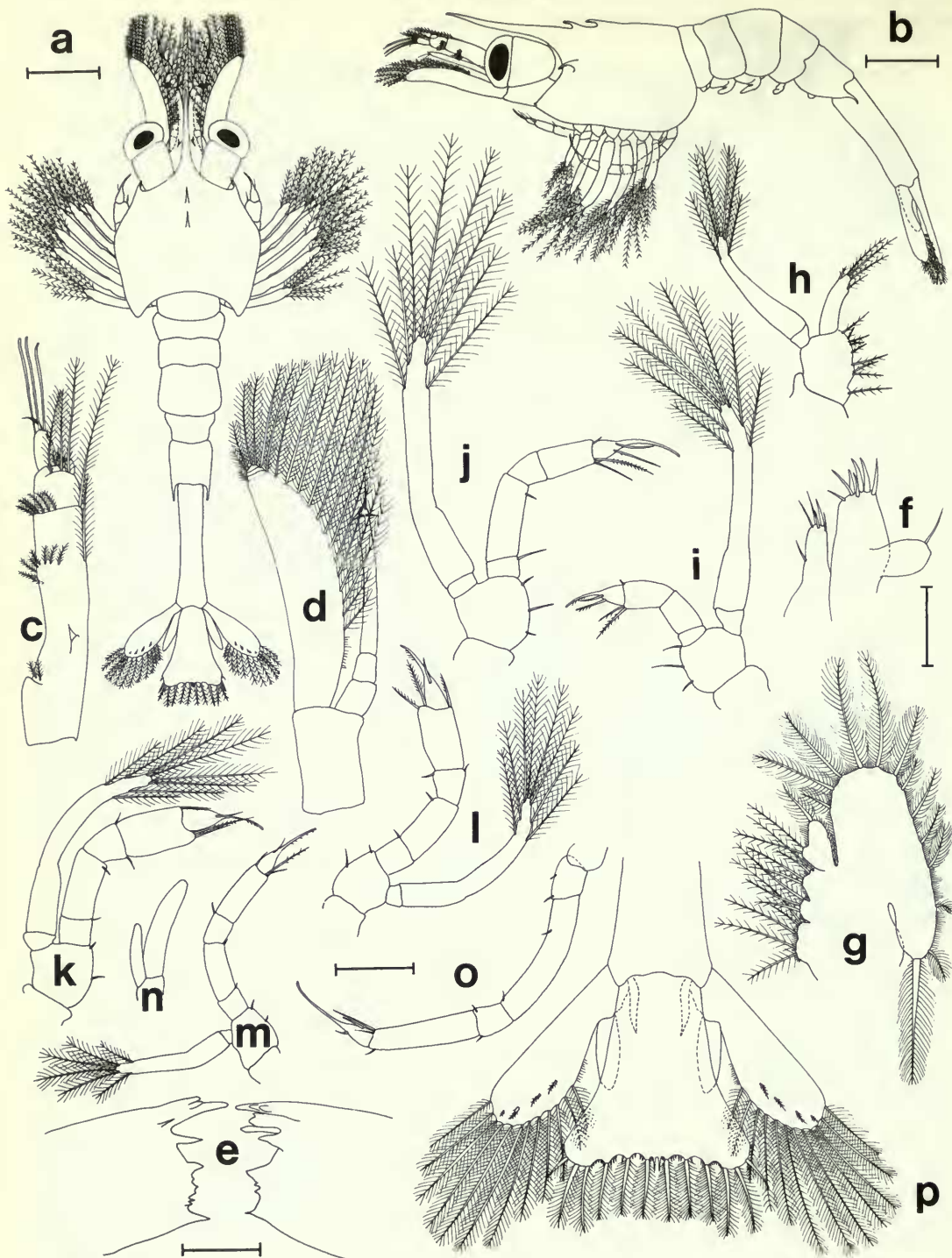


Fig. 3 Zoea 3: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandibles; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0.5 mm; c, d, h-p = 0.2 mm; f, g = 0.1 mm; e = 0.05 mm.

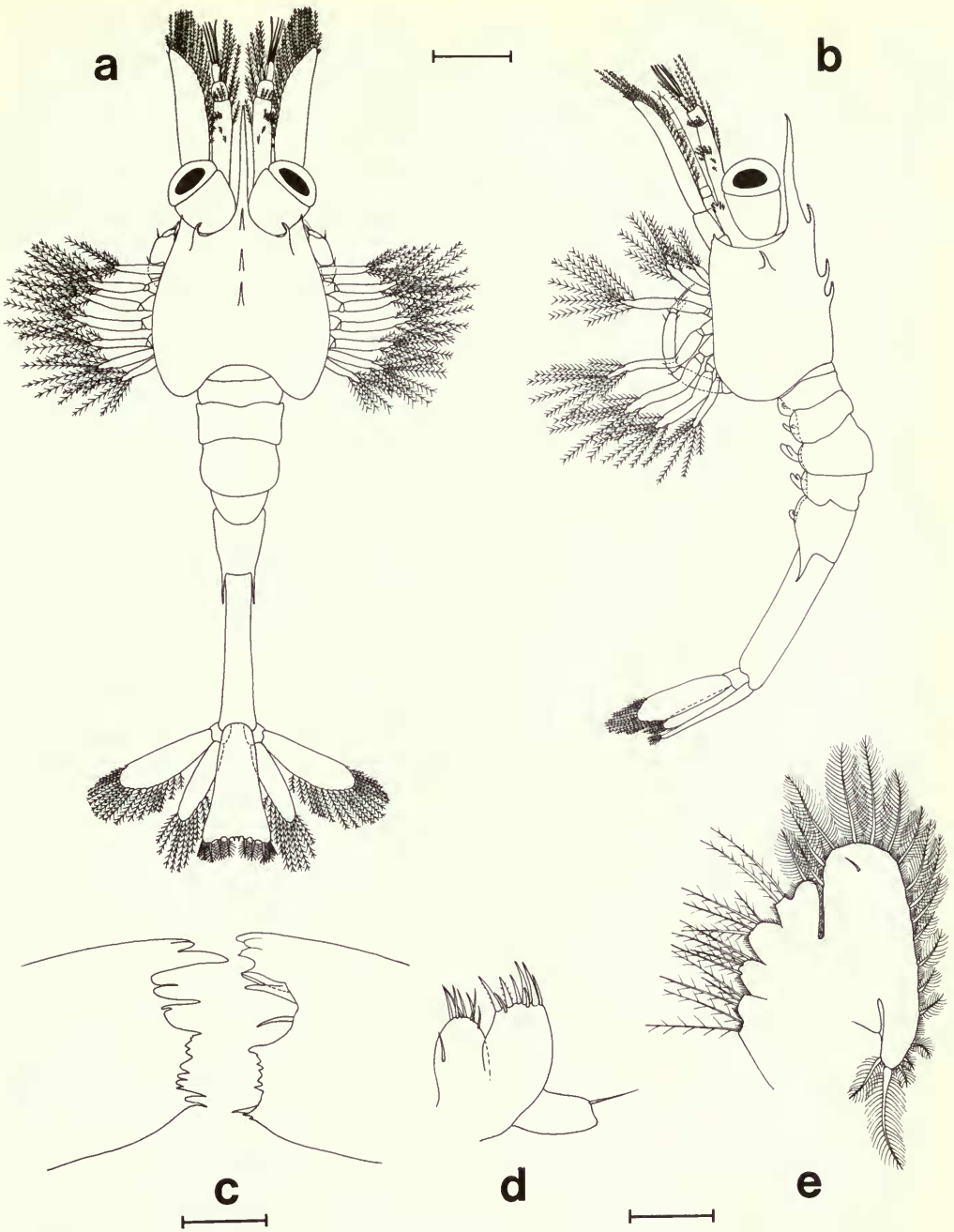


Fig. 4 Zoea 4: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2.
Bar scales: a, b=0.5 mm; c=0.05 mm; d, e=0.1 mm.

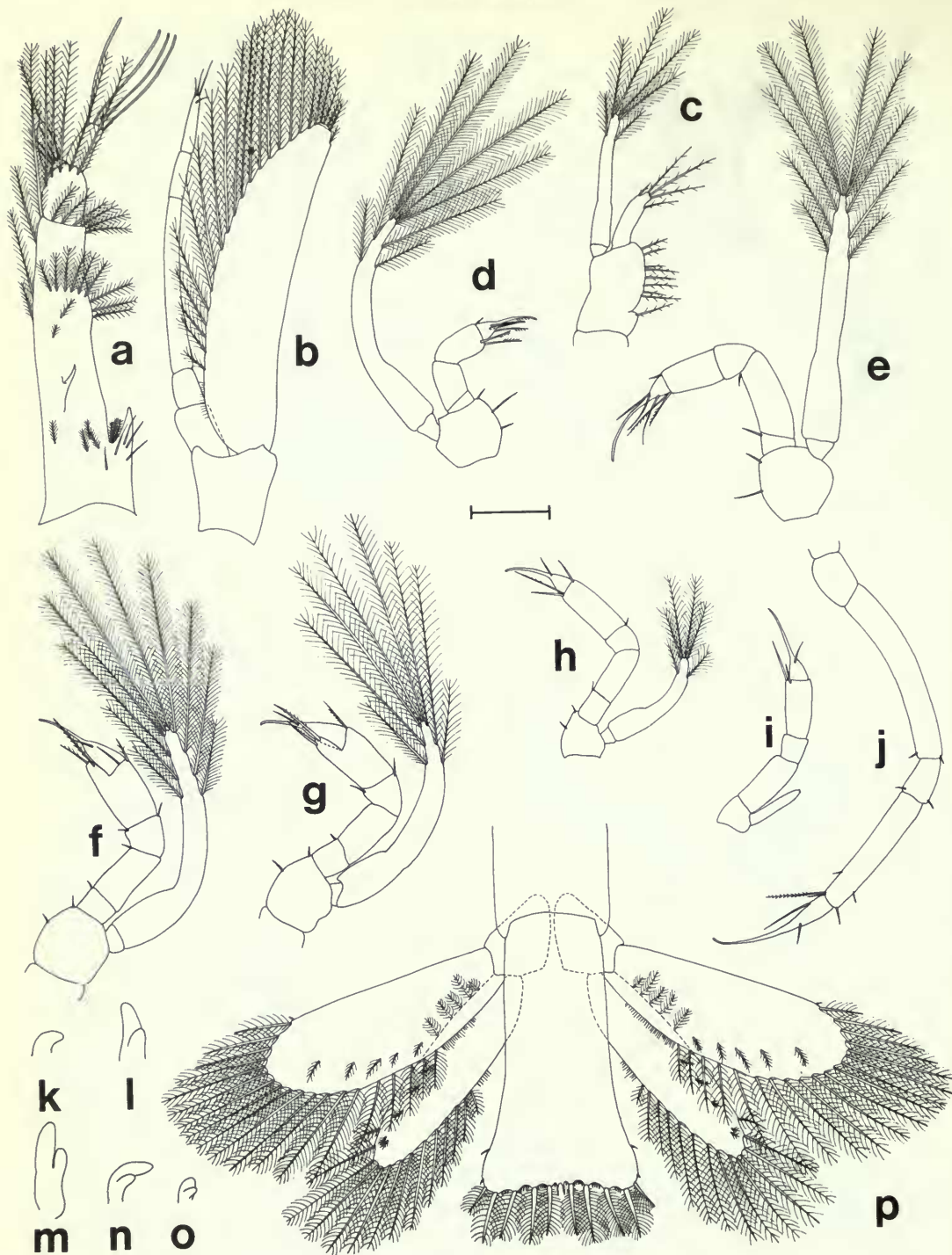


Fig. 5. Zoea 4: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) pleopod 1; (l) pleopod 2; (m) pleopod 3; (n) pleopod 4; (o) pleopod 5; (p) telson. Bar scale: a-p=0.2 mm.

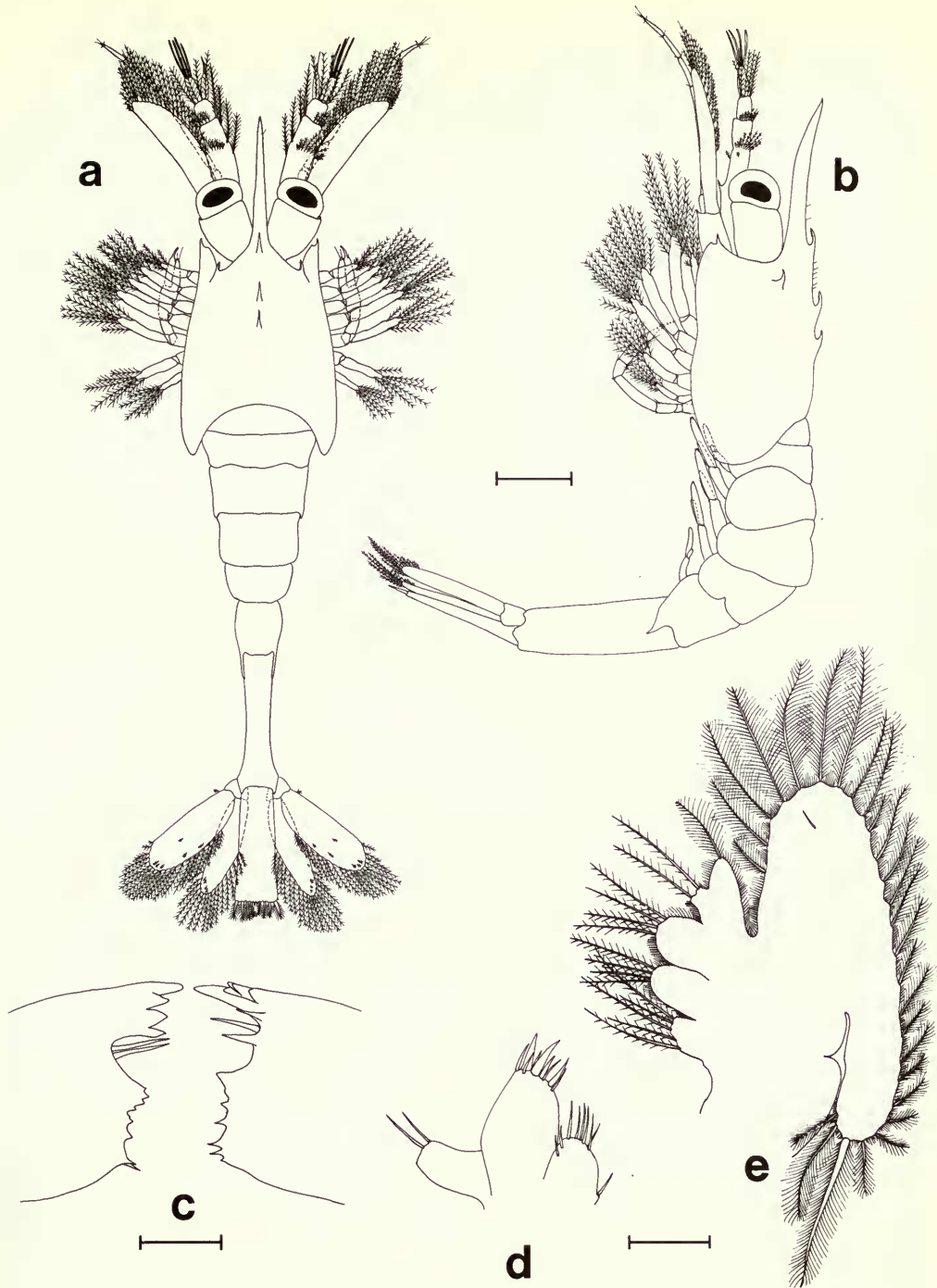


Fig. 6 Zoea 5: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b=0.5 mm; c=0.05 mm; d, e=0.1 mm.

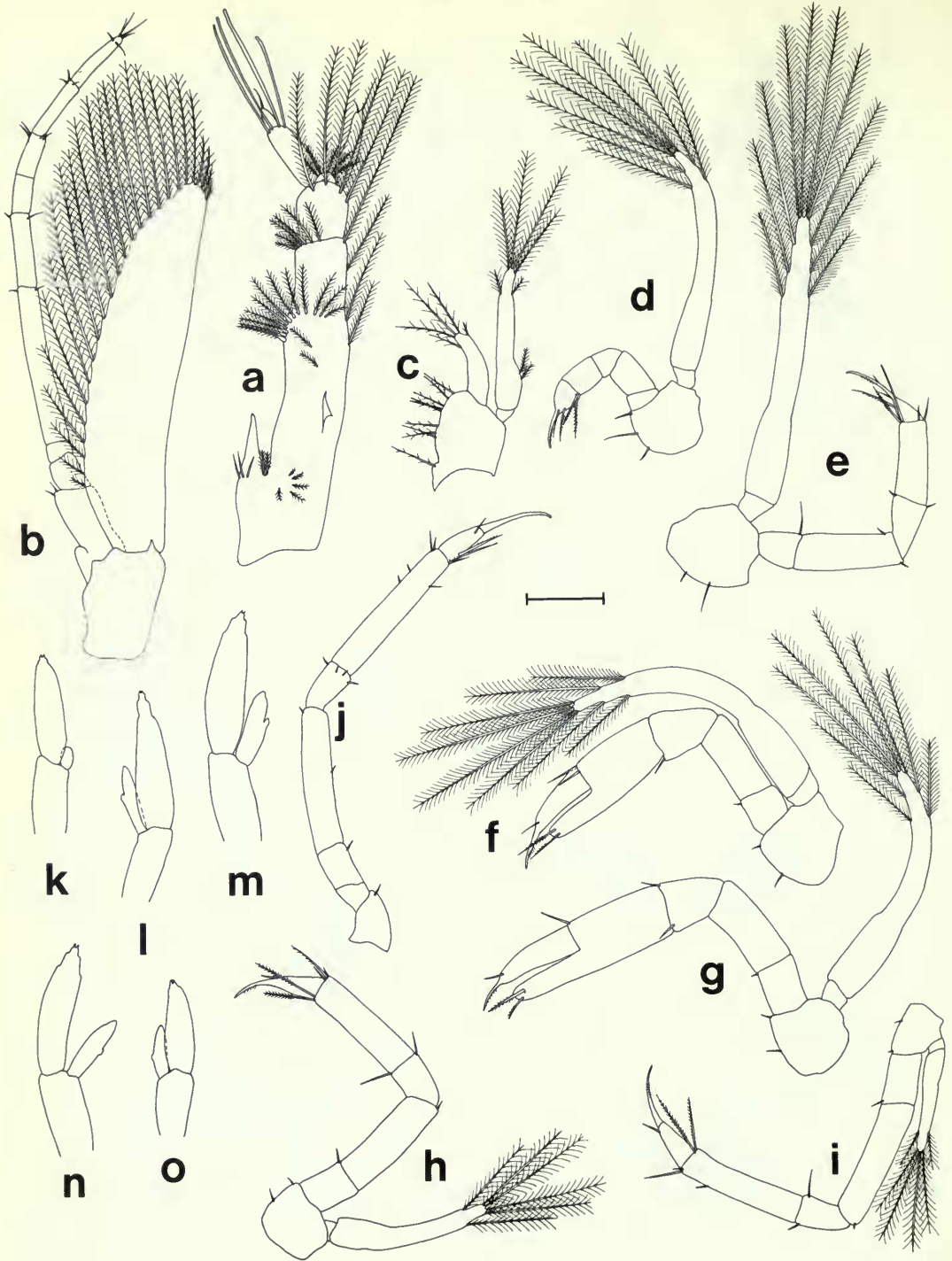


Fig. 7. Zoea 5: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) pleopod 1; (l) pleopod 2; (m) pleopod 3; (n) pleopod 4; (o) pleopod 5. Bar scale: a-o = 0.2 mm.

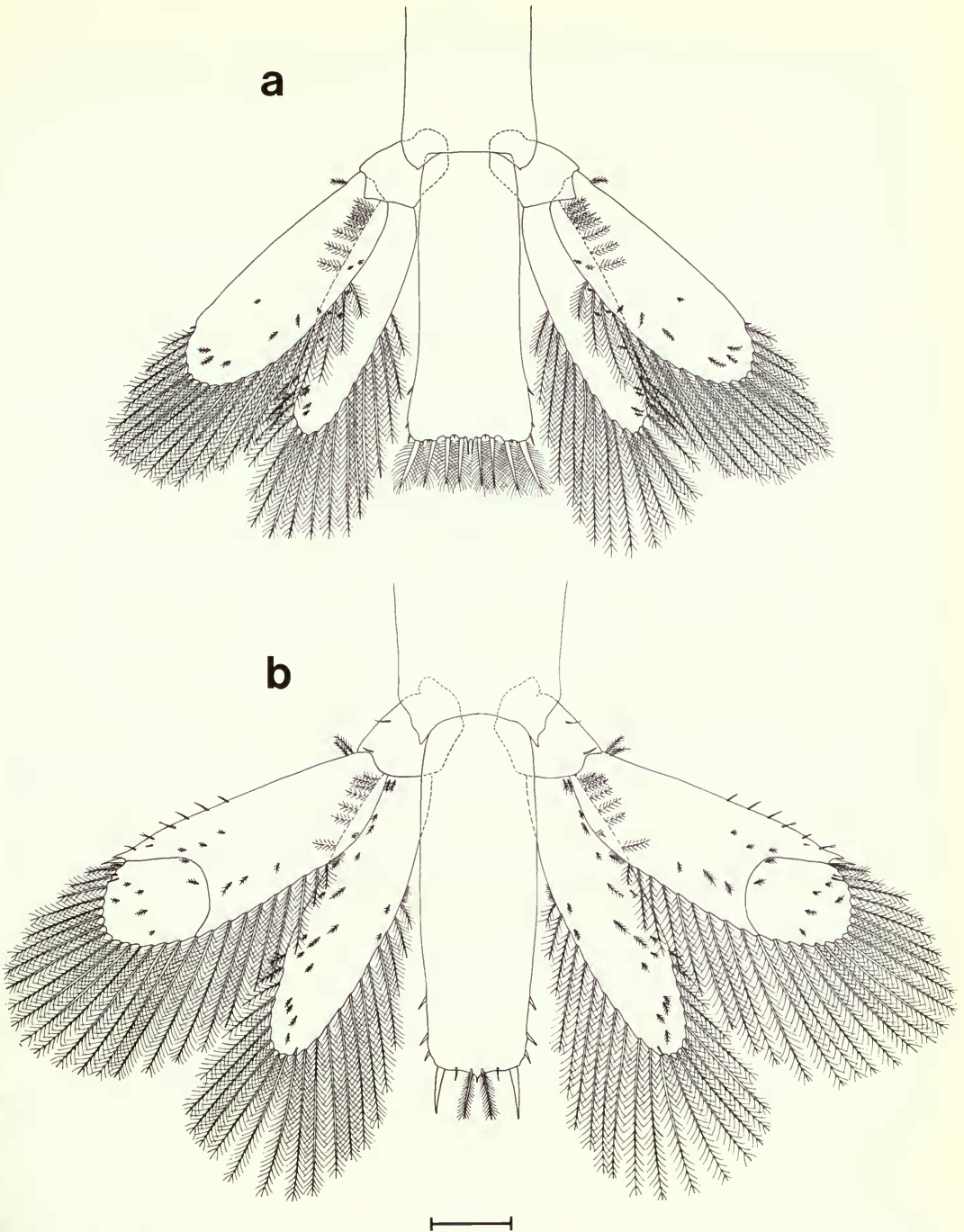


Fig. 8 Zoea 5: (a) telson. Post larva 1: (b) telson. Bar scale: a, b=0.2 mm.

Antenna (Fig. 7a): cirlet of plumose setae developed dorsally on first segment of peduncle, indicating position of statocyst.

Antenna 2 (Fig. 7b): *increase in number of segments of endopodite flagellum, just longer than scaphocerite.*

Pereiopods 1, 2 (Figs 7f, g): *endopodite with immovable finger of propodus produced forward to almost length of dactylus (excluding terminal setae).*

Abdomen (Figs 6a, b, 7k-o): *pleopods with rudimentary setae on margins of exopodite, endopodite of pleopods 2-5 with rudiment of appendix interna (stylamblyls).*

Telson (Fig. 8a): *with narrowing distally, posterior margin still weakly concave with 4+4 large spines and with 3 smaller spines on latero-distal margin.*

POST LARVA 1 (Figs 8, 9, 10, 11) 6.4 mm (6.0-7.0 mm)

Carapace (Figs 9a, b): *rostrum with 3-6 dorsal and 1-2 ventral spines, supraorbital spines missing.*

Antenna 1 (Fig. 10a): *internal flagellum of 2-4 segments and usually an additional group of 2 aesthetascs distally on first segment of external flagellum.*

Antenna 2 (Fig. 10b): *endopodite with flagellum multisegmented, more than twice length of scaphocerite.*

Mandible (Fig. 9c): *divided into pars incisiva and pars molaris, lacinia mobilis no longer present.*

Maxilliped 2 (Fig. 10d): *endopodite with dactylus, propodus and merus flattened, exopodite shortened and with no setae.*

Maxilliped 3 (Fig. 10e): *endopodite dactylus shortened, exopodite reduced to less than half length of endopodite, and without setae.*

Pereiopods 1, 2 (Figs 10f, g): *ischium, merus and carpus lengthened, exopodite reduced to about the length of the ischium of endopodite and with no setae.*

Pereiopods 3, 4 (Figs 10h, i): *endopodite dactylus evenly tapering distally, propodus, carpus and merus lengthened, exopodite reduced, extending halfway along ischium of endopodite, setae generally absent but with a few small, plumose setae sometimes present.*

Pereiopod 5 (Fig. 10j): *dactylus evenly tapering distally, other segments of endopodite lengthened.*

Pleopod 1 (Fig. 11a): *ratio of endopodite to exopodite 1:4, endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.*

Pleopods 2-5 (Figs 11b-e): *endopodite over half length of exopodite, both with long, marginal, plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hooks.*

Telson (Fig. 8b): *narrow, posterior margin convex with a short, median point, 1+1 large spines and two pairs of setae on the posterior margin, one long and plumose, other simple, also 3 smaller spines on latero-distal margin.*

POST LARVA 2 (Fig. 11) 7.2 mm (6.8-7.9 mm)

Maxillipeds, 2, 3: *exopodites lengthen and regain marginal, plumose setae.*

Pereiopods 1-4: *exopodites continue to diminish.*

Telson (Fig. 11g): *extremely narrow, median point on posterior margin more pronounced.*

POST LARVA 5 (Fig. 11)

Antenna 1 (Fig. 11h): *development of accessory flagellum on external flagellum.*

Antenna 2 (Fig. 11i): *morphogenesis of exopodite complete - truncated distally, edges almost parallel.*

Discussion

Results of the present study are summarized in Tables 1 and 2. The temporary regression of the exopodites of maxillipeds 2 and 3, in which shortening occurred with loss of marginal plumose setae and also the disappearance of the natatory exopodites of pereiopods 1-4, paralleled exactly the changes at first post larval moult (PL 1) for *Palaemon (Palaeander) elegans* (Fincham, 1977). The relatively abbreviated development of *Palaemonetes (Palaemonetes) varians* compared with the 6-9 stages of *Palaemon (Palaeander) elegans* is accompanied by a change in the sequence of

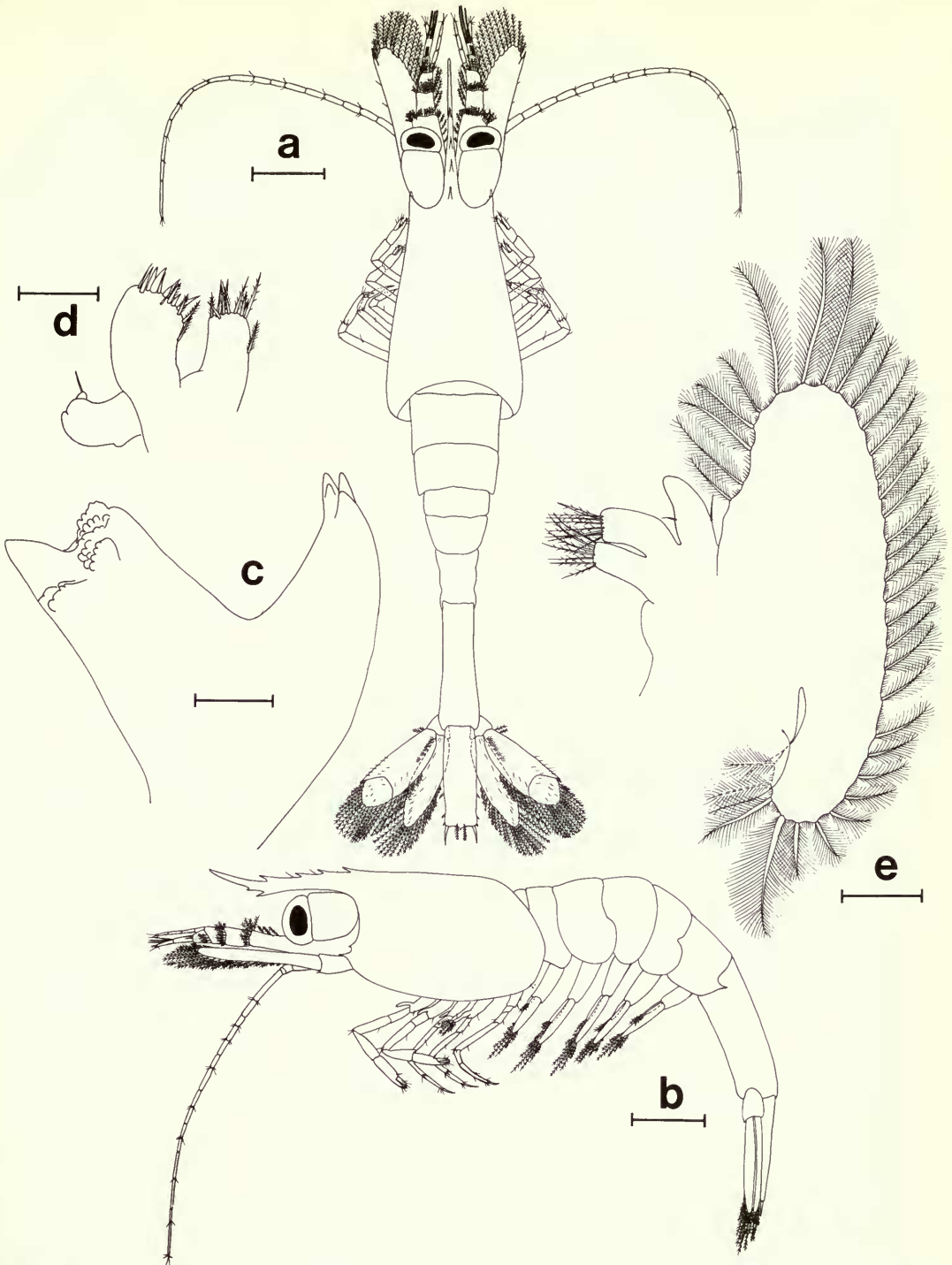


Fig. 9 Post larva 1: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2.
Bar scales: a, b=0.5 mm; c=0.05 mm; d, e=0.1 mm.

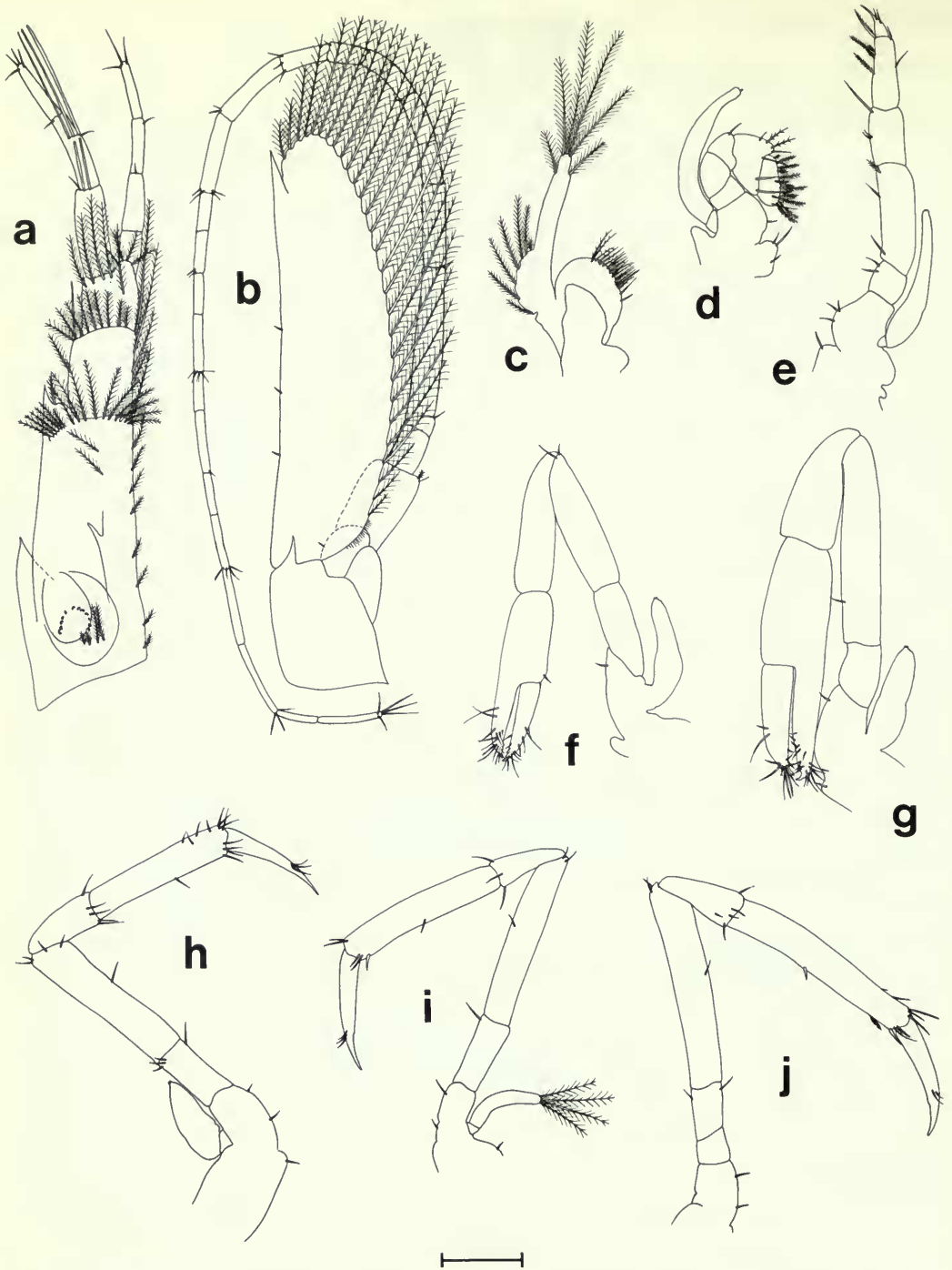


Fig. 10 Post larva 1: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5. Bar scale: a-j=0.2 mm.

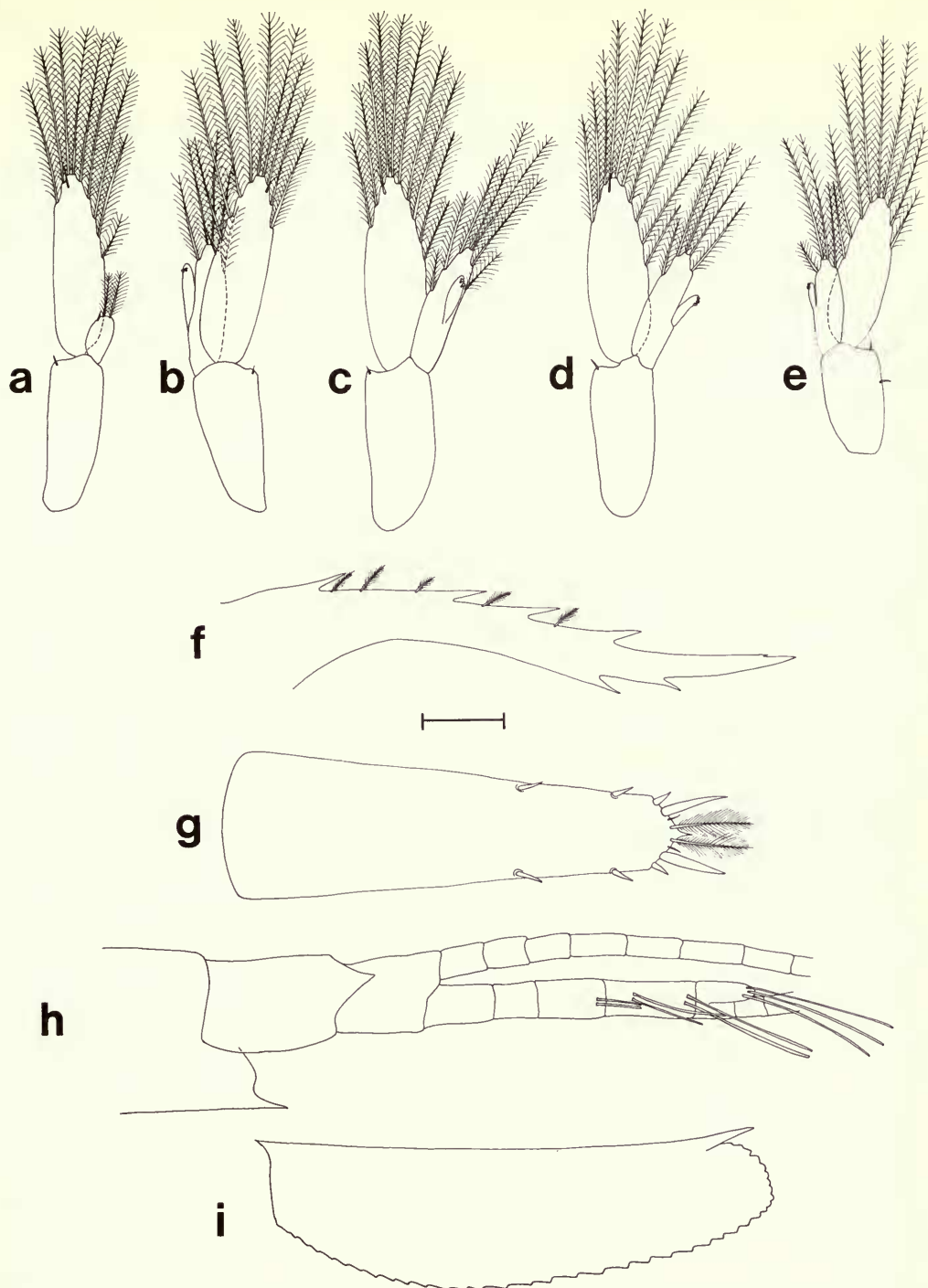


Fig. 11 Post larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5. Post larva 2: (f) rostrum; (g) telson. Post larva 5: (h) antenna 1 (aesthetascs drawn, setae omitted); (i) antenna 2 (setae omitted.) Bar scale: a-i=0.2 mm.

Table 1 Larval development and range of morphological variation in *Palaemonetes (Palaemonetes) varians*

		Zoea/Stage					
		1	2	3	4	5	PL1
	Mean Range	3.8 (3.5- 4.1)	4.2 (4.0- 4.5)	4.6 (4.3- 4.8)	5.2 (4.9- 5.5)	5.8 (5.5- 6.0)	6.4 (6.0- 7.0)
Carapace							
No. of dorsal spines		0	1	2	3	3	3-5
No. of ventral rostral spines		0	0	0	0	0	1-2
Supraorbital spines +/-		-	+	+	+	+	-
No. of antero-lateral spines		0	0	1	1	1	2
Rostrum tip - Ventral retrose hooks +/-		+	-	-	-	-	-
Antenna 1							
No. of groups, aesthetascs		1	1	1	1	1	1-2
Stylocerite +/-		-	+/-	+	+	+	+
Statocyst +/-		-	-	-	-	-	+
Medial spine +/-		-	-	+	+	+	+
No. of segments, flagellum - Internal		0	1	1	1	1	2-4
External		1	1	1	1	2	3-4
Accessory flagellum +/-		-	-	-	-	-	-
Antenna 2							
Endopodite - No. of segments		1	2	3	5	7-10	16-28
c.f. Length of scaphocerite		0.50	0.50	0.66 -0.75	1.0- 1.25	1.50- 1.75	2.0+
Exopodite - No. of distal segments		5	4	2	0	0	0
No. of plumose setae		9	16-18	18-21	21-23	23-26	24-32
External spine +/-		-	-	-	-	-	+
Mandible - Lacinia mobilis +/-		+	+	+	+	+	-
Maxilla 1							
No. of endite setae - Coxa		5-6	6	6-7	6-8	8-9	11
Basis		5-6	7	7-8	8-9	9	14
Maxilla 2							
No. of endite setae - Coxa		4-5	4-5	5	5-6	5	2
Basis 1		3	3	3	3-4	4-5	8
Basis 2		4	4	4	4	4-5	7
Endopodite		3-4	3-4	3	3	3-4	0
No. of plumose setae Exopodite		5-6	10-12	12-15	19-21	26-29	29-35
Maxilliped 1							
No. of setae on internal margin - Basis		5	8	9	9	9	19
Exopodite - No. of setae - Lateral (proximal)		0	0	0	0	2	7

pereiopod development. Limb buds were present in zoea 1, and at zoea 2 only pereiopods 3 and 4 were still rudimentary. At zoea 3 pereiopod 3 was fully developed together with a functional natatory exopodite, and at zoea 4 pereiopod 4 was fully formed also. The change to adult-type mandible (Fig. 9c) is made at the moult to PL 1 and is associated with the change in diet necessitated by the major behavioural change from a planktonic to largely benthic existence.

Table 1 (cont.)

		Zoea/Stage					
		1	2	3	4	5	PL1
Length (mm)	Mean	3.8	4.2	4.6	5.2	5.8	6.4
	Range	(3.5-4.1)	(4.0-4.5)	(4.3-4.8)	(4.9-5.5)	(5.5-6.0)	(6.0-7.0)
Maxilliped 2							
	Endopodite - No. of segments	4	4	4	4	5	5
	Exopodite +/-	+	+	+	+	+	+
	Setae +/-	+	+	+	+	+	-
Maxilliped 3							
	Endopodite - No. of segments	4	5	5	5	5	5
	Exopodite +/-	+	+	+	+	+	+
	Setae +/-	+	+	+	+	+	-
Pereiopods 1 & 2 +/-							
	Biramous +/-	R+	+	+	+	+	+
	Endopodite - Propodus fixed finger +/-	+	+	+	+	+	R+
		-	-	+	+	+	+
Pereiopod 3 +/-							
	Biramous +/-	R+	R+	+	+	+	+
		+	+	+	+	+	R+
Pereiopod 4 +/-							
	Biramous +/-	R+	R+	R+	+	+	+
		+	+	+	+	+	R+
Pereiopod 5 +/-							
	Biramous +/-	R+	+	+	+	+	+
		-	-	-	-	-	-
Abdomen							
	Somite 5 - Lateral spines +/-	-	+	+	+	+	+/-
	Somite 6 - Continuous with telson +/-	+	+	-	-	-	-
Pleopods +/-							
	Fringing setae	R+	R+	R+	R+	+	+
	Appendix interna 2-5 +/-	-	-	-	-	R+	+
Telson							
	Posterior margin concave (-) convex (+)	+/-	+/-	-	-	+/-	+
	Spine formula	7+7	7+7	6+6	5+5	4+4	1+1
							(PL2:2+2)
	Small spines +/-	+	+	+	+	+	-
	No. of pairs - Lateral spines	0	0	1	2	3	3
							(PL2:2)
	Uropods +/-	-	-	+	+	+	+
	Long plumose setae - Endopodite			0	10-14	16-18	18-22
	Exopodite			11-13	17-20	20-23	21-26

Rate of epigenesis

In order to transform zoea 1 to a miniature adult or juvenile, a definite sequence of morphogenetic and associated biochemical and physiological development and adaptation has to be completed. If larvae moult 'early', less of the developmental sequence is completed. Epigenesis in Crustacea is a continuous sequential process despite being apparently arrested at morphological

Table 2 Analysis of morphometric variation (a) in overall size in mm and meristic variation in the number of exopodite plumose setae of (b) antenna 2, (c) uropod and (d) maxilla 2 during the development to post larva of *Palaemonetes (Palaemonetes) varians* (n.d.=not developed; see Materials and Methods for statistical abbreviations)

	Stage					
	1	2	3	4	5	PL1
a \bar{x}	3.82	4.24	4.55	5.19	5.77	6.41
s.d.	0.21	0.18	0.14	0.17	0.18	0.32
c. of v.	5.49	4.19	3.15	3.20	3.06	5.01
b \bar{x}	9	17.0	19.5	22.3	25.2	27.4
s.d.	0	0.82	1.08	0.67	0.92	2.37
c. of v.	0	4.80	5.54	3.03	3.65	8.64
c \bar{x}	n.d.	n.d.	12.2	18.6	21.6	23.7
s.d.	—	—	0.79	0.97	1.26	1.64
c. of v.	—	—	6.47	5.19	5.86	6.90
d \bar{x}	5.6	10.6	13.4	19.7	27.5	31.7
s.d.	0.52	0.70	1.17	0.67	1.35	2.06
c. of v.	9.22	6.60	8.76	3.43	4.92	6.49

stages during the intermoult period of ecdysis. Moulting and epigenesis become desynchronized after the first few zoeal stages. This results in morphological variation in larvae with similar moulting histories (in terms of the number of moults), but in which epigenesis may have been proceeding at different rates. Also, the longer an intermoult period lasts so the next stage is more advanced. Superimposed on this is normal intraspecific variation including variation within a brood from one female.

The separate control of development and moulting is adaptive in that larvae are able to cope with sub-optimal conditions by slowing epigenetic development while continuing to moult. The animal is constrained physically by the rigid exoskeleton and moulting is essential to permit an increase in size. Epigenesis may be delayed, but moulting continues and may not always be accompanied by an increase in size. This results in so called 'repeat' moults (Rochanaburanon & Williamson, 1976; Fincham, 1977). As moulting uses up energy and increases vulnerability until the exoskeleton hardens after ecdysis, it is reasonable to assume that moulting has functions other than merely allowing an increase in size. It is not clear why moulting does not cease in poor conditions. It has been shown, from analysis of whole larvae, that organic substances including proteins and amino acids and inorganic ions such as K^+ , Ca^{++} , Mg^{++} rise in concentration during premoult and decrease at postmoult, and the reverse occurs in concentrations for Na^+ and Cl^- (Torres, 1973; Charmantier, 1977). The periodic release into the haemolymph of these molecules and ions may be necessary to make them available for stages in the epigenetic sequence. This leads to the development of the new structures, which in the larval stages is continuous even if, in response to poor external environmental conditions, the rate is slow.

Meristic and morphological variation (Tables 1, 2)

In a study of morphological variation in natural populations of the smooth newt, Bell (1974) found that animals of average length survive in conditions of stress such as the critical period of metamorphosis. As the total length increases, therefore, so variation in this character would be expected to decrease. Waddington (1948) pointed out that development is canalized with a strong tendency for the adult to conform to the morphological norm within prescribed limits. In a later paper Waddington (1953) discussed the inflexibility of the biochemical pathways controlled by the epigenotype during development. These pathways lead inevitably to a similar end result, to a

large extent regardless of unfavourable influences from the genotype or the environment. Bell (1974) stated that '... the epigenetic system is so constructed that individuals which are originally quite different tend to become more similar as their development proceeds'.

Both developmental canalization (stabilizing selection) and natural (normalizing) selection have the effect of reducing variation. Bell (1974), however, was able to eliminate the former in accounting for the decrease in variation in the two morphometric characters (standard length and head width) as the larvae approached metamorphosis. This was achieved by keeping laboratory populations of newt larvae in near optimum conditions. Overall survival was better than for equivalent wild populations since external natural selection was less intense in the laboratory, whereas the internal stabilizing selection would have been the same in both wild and laboratory populations. This reduction in variation of larval size distribution was reversed in post-metamorphosis newts and was corroborated by dentition data (Bell, 1975). The obvious advantage of such selective processes is that only typical representatives of the species survive metamorphosis.

The present morphometric results (Table 2) parallel the findings of Bell and show that there is a significant reduction ($P < 0.05$) in variation or normalizing selection of larval size as *Palaemonetes* (*Palaemonetes*) *varians* approached metamorphosis, with a tendency to increase in post-metamorphosis shrimps. All other correlations of meristic characters were not significant and there was no tendency for individuals to become more similar as suggested by Bell (1974). Particular attention was given to the shrimp mouthparts since Bell (1975) found newt dentition data corroborated his morphometric findings. To compare these results of *Palaemonetes* (*Palaemonetes*) *varians*, data (Fincham, 1977) from a closely related palaemonid *Palaemon* (*Palaeander*) *elegans* was analysed to test for changes in variation as metamorphosis approached. In the latter species even morphometric data were not significant. There was, however, a significant increase in variation of the plumose setae on the exopodite of mouthpart maxilla 2 in the pre-metamorphosis stages ($P < 0.01$). Clearly there is no simple, general correlation between larval variation and the approach of metamorphosis.

Some similarities in habitat exist between the newt and *Palaemonetes* (*Palaemonetes*) *varians*: both live in shallow ephemeral bodies of water and both showed a reduction in overall length variation. A rigorous selection process may be necessary to ensure survival in this particular habitat. The increase in variation of maxilla 2 in *P. (P.) elegans* – a genuine increase and not simply a corollary of increased size – presents a totally unexpected reversal of normalizing selection. This shrimp is a common inhabitant of intertidal rockpools and undergoes 6–9 zoeal moults before metamorphosis. The larvae are planktonic and have access to a wide variety of coastal habitats when they become benthic after the final larval stage. There is a degree of uncertainty in making immediate contact with the most suitable rocky coastline and a degree of variation would clearly be advantageous.

Gurney (1924) stated '... a knowledge of the larval history is of importance in tracing the systematic relationships of Decapoda ...'. One of the aims of this present series of papers is to provide detailed descriptions of larval stages to aid identification and to form the basis of a systematic study using numerical methods. For this purpose the extent of larval variation needs to be determined. Gurney (1924) gave details of intermediate post larval stages in which various combinations of late larval and first post larval characters were found. While these were not unknown in the present study, rearing at 22 °C produced a rapid, and in most cases direct, development to PL1 through five larval stages. The delay in the epigenetic process recorded by Gurney was probably a response to environmental stress imposed by the rearing techniques. With regard to larval polymorphism or poecilogony (Boas, 1889; Heldt, 1953) abundant larval variation was recorded in the present study but this did not exceed variability commonly found in larval prawns and shrimps.

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